Some factors influencing the prevalence of Endothia gyrosa

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(with five text figures)

Introduction

The distribution of the American species of *Endothia* does not coincide with that of their hosts. Range maps of these species made by Dr. C. L. Shear and the writer as the result of two years collecting, show that *Endothia gyrosa* (Schw.) Fries is abundant in the Southeastern States and has been found occasionally as far north as southern Connecticut and western New York, while two of its hosts, *Fagus* and *Quercus*, occur several hundred miles further north. *Endothia fluens* (Sow.) S. & S., which is common on *Castanea* and *Quercus* from northern Alabama to southern Pennsylvania, has not yet been found north of this region. The territory between Virginia and southern New England appears then to be a transition region for these fungi. Examination of these maps also shows that *Endothia singularis* (H. & P. Syd.) S. & S. and *E. fluens* occupy fairly well defined climatic areas and are apparently not found in America outside these areas. *Endothia gyrosa*, however, while abundant only in the Southeastern States, has been found in Connecticut, New York, Kansas, Texas, and on the Pacific Coast.

The present paper deals with *Endothia gyrosa*, which has a much wider known range in America than any other species of the genus. This fungus is undoubtedly indigenous, having first been collected by Schweinitz at Salem, North Carolina, nearly a century ago, and previous to recent work had been collected at various times in the following widely separated localities: Indiana, 1831 (?), *Schweinitz;* Texas, 1869, *Ravenel;* New York, 1872, *G. W. Clinton;* Florida, 1886–87, *Calkins;* Mississippi, 1887, *Earle;* Kansas, 1887, *Swingle;* Louisiana, 1887, *Langlois;* New Jersey, 1892 (?), *Ellis.*

The intensive collecting of the last few years has not greatly

extended the range of *Endothia gyrosa* beyond that known twenty-five years ago. It may therefore be fairly assumed that this fungus has reached its natural limits of distribution in this country and that the present range is determined by environmental factors, in contrast to fungi which have been recently introduced and have therefore not yet spread throughout the region suitable for their development.

In collaboration with Dr. Shear the writer has prepared a map (FIG. 1), which gives a somewhat more accurate idea of the

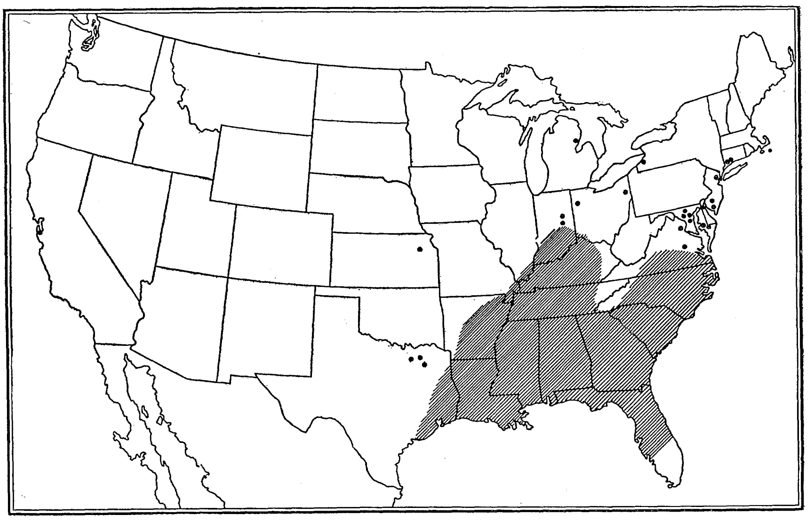

FIG. 1. Known distribution of *Endothia gyrosa*. Cross hatching indicates area in which the fungus is known to be abundant. Dots indicate localities where it has been collected. Map prepared by the writer in collaboration with Dr. C. L. Shear.

distribution of *Endothia gyrosa* than that previously published. The cross hatching indicates the area in which the fungus is known to be abundant, the dots outside that region indicate localities in which the fungus has been collected. In considering the distribution of *E. gyrosa* the problem is double, for the fungus has been found at widely separated localities hundreds of miles outside the region in which it is common. Conditions under which it can exist are not then, necessarily, those under which it will become abundant. The conditions which limit the occurrence

of this fungus have not yet been discovered. The following notes indicate certain factors which seem to influence its prevalence within its present range. In discussing this question observations are confined to the eastern half of the United States, where most of the collecting was done and where, consequently, the distribution of the species is fairly accurately known. This area is particularly favorable for a study of the climatic relations of fungi since, as Ward (**11**) has pointed out, it constitutes a single climatic subdivision of the country.

INOCULATION EXPERIMENTS

In connection with work already reported (**10**), inoculations of *E. gyrosa*, *E. fluens* and *E. fluens mississippiensis* were made at various points from Charlottesville, Virginia, to Concord, New Hampshire, in the hope that data might be obtained concerning the effect of climate on their growth. The inoculations were located at points chosen for their availability and their nearness to United States Weather Bureau Stations. These places were visited every five or six weeks during the summer of 1914, twice during the summer of 1915, and once in May, 1916. At each visit ten or more new inoculations were made on species of *Quercus* (sometimes also on *Fagus*) using the method described for previous work (**8**, **10**), and notes were made on the condition of the earlier inoculations. TABLE I gives a brief summary of the results of the observations on *E. gyrosa*.

The results of these inoculations have emphasized four facts, already known. Black oaks (*Erythrobalanus* Spach.) are much more favorable for the growth of *E. gyrosa* than white oaks (*Lepidobalanus* Endl.). *E. gyrosa* will under certain conditions grow and winter over as well near or beyond the northeast limits of its known range as it will within the region where it is most abundant. Water supply is important in the growth of the fungus. The condition of the host is important; this may be, at least in part, only another indication of the importance of the water supply, as obviously the water necessary for growth may be supplied by the host or by the atmosphere.

An examination of the table shows that *Endothia gyrosa* survived the winters of 1914–1915 and 1915–1916 without apparent

TABLE I

Locality	Inoculations made	Pycnidial stromata appeared	Further notes
Charlottesville, Va.	April 20 and May 21, 1914.	Oct. 2, 1914. Abundant especially on tree inoculated May, 1914.	The small tree on which the inoculations of May 1914 were made died during the summer from partial girdling at the time of inoculation. Apparently as a result of this the fungus developed rapidly and produced pycnidial stromata for a distance of 10–12 in. above the point of inoculation.
Fairfax, Va.	April 21 and Aug. 1, 1914.	July, 1914, a few pycnidia on the injured tissue above the inoculations of April. Oct. 24, 1914, fairly abundant and well developed on inoculations of both dates.	
Frederick, Md.	May 30, 1914.	May 21, 1915.	There was no evidence of growth from these inoculations during the summer of 1914. Pycnidia, however, appeared on one branch in the spring of 1915.
Woodstock, Md.	May 30 and July 30, 1914.	Oct. 19, 1914.	While both these inoculations showed considerable development of pycnidial stromata they were less than some others both further north and further south.
Wilmington, Del.	July 6, 1914.	Oct. 6, 1914.	Large well-developed stromata, which showed no change during the succeeding summer.
Hartford, Conn.	July 15, 1914. Sep. 24, 1914.	Sept. 23, 1914. A very few stromata. Aug. 18, 1915, large well-developed stromata.	In this case stromata developed abundantly during the summer of 1915 from inoculations which during the summer of 1914 showed only a few scattering stromata.
Amherst, Mass.	July 15, 1914.	Sept. 24, 1914.	This inoculation became contaminated later with *Endothia parasitica*.
Williamstown, Mass.	July 14, Sept. 24, 1914, & May 21, 1915.	Aug. 16, 1915.	The small oak on which the inoculations of July 1914 were made was killed by the cuts and bore numerous large pycnidia of this fungus during the summer of 1915. None of the inoculations made at this point produced stromata during the summer of 1914.

TABLE I—*Continued*

Locality		Inoculations made	Pycnidial stromata appeared	Further notes
Concord, N. H.		Sept. 22, 1914 May 18, 1915.	Aug. 19, 1915.	Several good sized pycnidial stromata developed on several of the inoculations of both these dates.
Stations on Overlook Mt., Woodstock, N. Y.				
Station	Elevation in feet			
S 3	1,000	June 12, 1914.	Aug. 14, 1915.	Pycnidial stromata appeared from one inoculation during the summer of 1915, though there had been no evidence of development during the summer of 1914.
C	1,500	June 13 & Sep. 30, 1914.	Aug. 11, 1915.	Abundant large pycnidial stromata developed during the summer of 1915, although none had developed during the summer of 1914.
O 6	1,500	June 11, Jul. 8, Aug. 12, 1914.	May 25, 1915. From inoculations of June, 1914; and Aug. 12, 1915, from inoculations of July and Aug. 1914.	
O 1	1,900	June 11, 1914. July 9, 1914.	Sept. 29, 1914.	These showed the greatest development of any stromata of *E. gyrosa* in the entire series of inoculations. Abundant pycnidial stromata developed extending 1–6 in. above and below the cut in each inoculation. There was continued growth but no perithecia had developed up to May 1916.
O 4	2,800	July 9, 1914.	May 26, 1915.	Numerous stromata developed well beyond the cut and extending for a foot or more above and below the place of inoculation. These were alive and in good condition May 1916, but had produced no perithecia.

All the inoculations listed above as having developed pycnidial stromata were alive in May, 1916, but no perithecia had developed.

injury in the most northern localities at which inoculations were made, i. e., Williamstown, Massachusetts, and Concord, New Hampshire, and at an elevation of 2,800 feet on Overlook Moun-

tain. Its growth in these localities was nearly, if not quite, equal to that at more southern points.

The effect of abundant moisture is readily seen from the fact that at Concord, Williamstown, and two stations, S 3 and C, on Overlook Mountain, stromata developed in 1915 from inoculations which had shown no growth in 1914; as well as by the fact that at Hartford, Connecticut, stromata developed abundantly during the summer of 1915 from inoculations which during the summer of 1914 showed only a few scattered stromata. As the weather conditions of the two summers in these localities have been discussed in detail by the writer elsewhere (10) it may merely be stated here that there was little difference in the temperature but that the rainfall of 1914 was much below normal; that of 1915 well above normal.

The importance of the condition of the host in the growth of *Endothia gyrosa* was best seen at Charlottesville, Virginia,* where the small tree which was inoculated gradually died from the effect of the cuts and the fungus developed rapidly and produced stromata for a considerable distance above and below the point of inoculation. The growth of the fungus on this tree was much greater than that on any of the trees which survived the wounds made by inoculations. The peculiar relations between this fungus and its host have been referred to elsewhere (8). In general it has been observed that tissue injured by cuts or bruises in such a way that it does not dry out immediately but remains in a living condition for some time is the most favorable place for the development of this fungus. Such a condition is found on the stubs of cut limbs, on bruised or broken trunks, and especially on exposed roots which have been injured by tramping of cattle or by other means. This habit of the fungus seems to materially affect its distribution.

CLIMATIC RELATIONS

Temperature.—The range of temperature favorable for the growth of *E. gyrosa* in artificial media seems to be almost identical with that of *E. parasitica* (8). The writer has recently demonstrated (10) that during the years ending in May and August,

* The inoculations and some of the observations at this point were made by G. F. Gravatt.

1915, *Endothia parasitica* made almost twice the lateral growth on *Castanea dentata* in Virginia that it made in New England. This difference in growth is closely correlated with the difference in temperature of the two regions. It seems very probable, therefore, that the more favorable temperature of the Southern States favors the more abundant growth of *E. gyrosa* in that region.

A comparison of the map (FIG. 1) of the distribution of *E. gyrosa* with climatic maps shows certain general correlations. Much of the region where *E. gyrosa* is most abundant lies south of the isotherm of 6,000 temperature summation and the closely similar isotherm of 600 temperature efficiency as calculated by the Livingstons (**7**). Much of the region where *E. gyrosa* is most abundant lies within or south of the area of eight months (April to November) vegetation, as mapped by Zon (**12**).

It is significant, however, that the area in which *E. gyrosa* is abundant does not agree closely with any of these lines. The fungus is abundant considerably north of the line of 600 temperature efficiency in Kentucky and southern Indiana but falls far short of this isotherm in eastern Virginia. The same relation exists between the area in which *E. gyrosa* is abundant and the isotherm 10,000 as given by Livingston (**6**) in his chart based on physiological summation indices of temperature efficiency for plant growth (**6**, *f. 2*). Similarly, the northern limit of the area of abundance coincides closely with the limit of eight months vegetation in Virginia, but runs well toward the middle of the area of seven months vegetation in Kentucky and Indiana. Moreover, as has been stated above, the temperature of New England in the region of six months vegetation is evidently sufficient for the growth of *E. gyrosa* under some circumstances.

On the other hand, *Endothia gyrosa* is not perceptibly more abundant in the areas of nine to twelve months vegetation, i. e., southern Mississippi, Alabama, and Florida, than it is in certain portions of the area of seven months vegetation, i. e., Kentucky and southern Indiana. It would seem then that temperature alone is not very significant in determining the abundance of this fungus.

Precipitation.—One of the most important climatic factors influencing the abundance of *E. gyrosa* in the Southern States is

probably the greater rainfall, especially during the growing season. The rainfall of the eastern United States during the growing season is given by Henry (5). In general, the area where *E. gyrosa* is abundant is largely in or south of the region of twenty-five inches rainfall, April to September, inclusive. An exception to this is found in Tennessee, Kentucky and southern Indiana, which are well outside the area of twenty-five inches rainfall, but where *E. gyrosa* is fully as abundant as in the region of over thirty inches rainfall.

The striking fact has recently been pointed out by Ward (11), that in the eastern United States no sudden changes in climate are met with in going from north to south, but the transitions are everywhere slow and gradual. On the other hand, there is a fairly definite line of demarcation between the area in which *E. gyrosa* is abundant and the area where it is rare. This seems to indicate that factors other than temperature and rainfall markedly affect the prevalence of this fungus.

That *E. gyrosa* is abundant in southern Indiana where the climate is both drier and cooler than in most regions where the fungus is commonly found, seems to be due to greater opportunity for infection. As has been pointed out in an earlier paper (8), southern Indiana is a stock-raising region where pastures containing beech trees are numerous. Nearly all of the collections of *E. gyrosa* in this region were found in such pastures on the roots of beech which had been injured by cattle. The importance of such opportunity for infection is emphasized by the condition found at Columbiana, Ohio, in June, 1913. This locality is several hundred miles outside the area in which *E. gyrosa* is commonly found in abundance, yet in a single pasture where there were from fifteen to twenty large beech trees many of whose roots were exposed and had been injured by trampling of cattle, the writer found this fungus abundant in more than twenty small patches.

OPPORTUNITY FOR INFECTION

Field observations have convinced the writer that opportunity for the infection of its hosts is of the greatest importance in determining the prevalence of *E. gyrosa* and that the greater abundance of *E. gyrosa* in the southern states is largely accounted for by the

greater opportunity for infection in that region, aided by more favorable temperature and more abundant rainfall. Other things being equal, the more frequent the occurrence of places favorable for its growth the more abundant a fungus will become. This process is cumulative, for the more prevalent a fungus the more completely it will occupy the available places of infection.

Greater opportunity for infection in the south is due to the greater number of host species and to the greater importance of these species relative to other trees. And especially to greater opportunity for the infection of individual hosts from injuries due to different climatic, soil and cultural conditions.

HOST RELATIONS

Endothia gyrosa is found commonly in the United States on hosts of four genera: *Castanea*, *Fagus*, *Liquidambar*, and *Quercus* —least abundantly on *Castanea*, most abundantly on *Quercus*— the collections made in the work already referred to (**8**) being in the following numbers: *Castanea*, 18; *Fagus*, 47; *Liquidambar*, 49; *Quercus*, 158. Actually the fungus is much less frequent on *Castanea* than is indicated by these figures, since the eighteen collections represent all the cases in which *E. gyrosa* was found on *Castanea*, while the number of collections on the other hosts represent simply a few specimens from each locality visited and could have been increased many times.

Endothia gyrosa has been collected by Dr. Shear and the writer on the following species of *Quercus: Q. alba* L., *Q. coccinea* Muench., *Q. digitata* (Marsh.) Sudworth, *Q. georgiana* Curtis, *Q. imbricaria* Michx., *Q. marilandica* Muench., *Q. nigra* L., *Q. phellos* L., *Q. Prinus* L., *Q. rubra* L., *Q. velutina* Lam., *Q. virginiana* Mill. From the first, however, it was obvious that the fungus was more abundant on the various species of black oaks than on the species belonging to the white oak section of the genus. Of the 158 specimens from all parts of the United States which were collected, eighty are known to be on species of black oak, nineteen on species of white oak. The specimens, for which the host species is not given, are apparently divided in about the same ratio. These unidentified specimens are chiefly from the southern states where the collecting was done largely in midwinter.

RANGES OF HOST SPECIES

The maps, FIGS. 2–4, show the ranges of the various host species: FIG. 2, the ranges of *Castanea, Liquidambar* and *Fagus;* FIGS. 3 and 4, the ranges of the species of *Quercus* on which *E.*

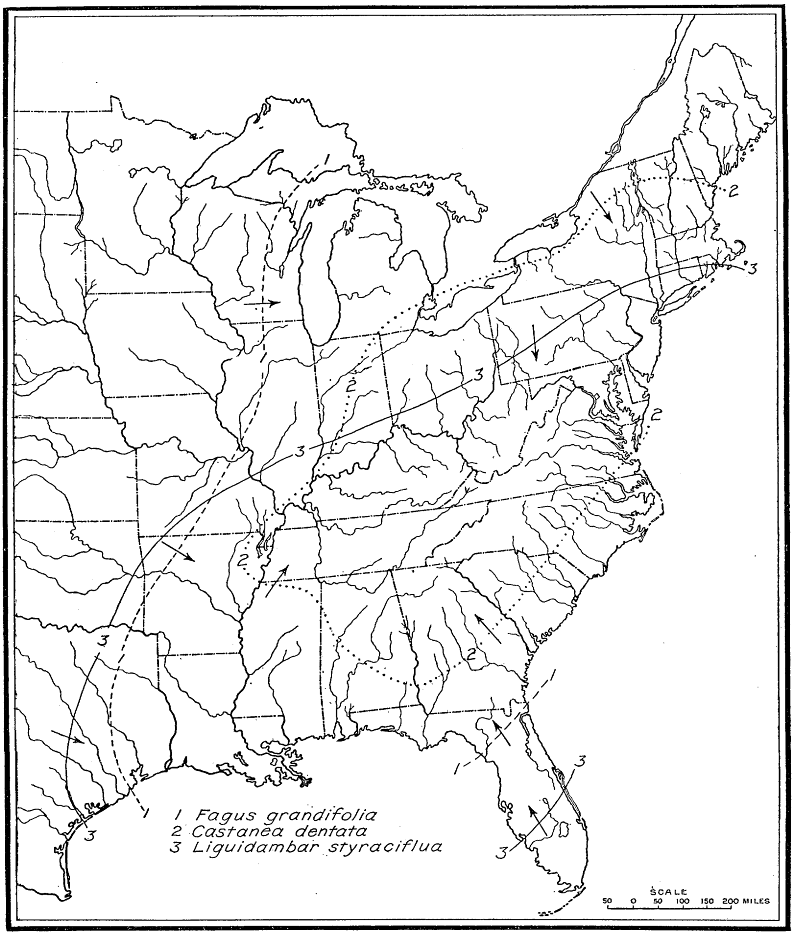

FIG. 2. Ranges of *Fagus grandifolia*, *Castanea dentata*, and *Liquidambar Styraciflua* in the United States. Map prepared by W. H. Lamb, United States Forest Service.

gyrosa is known to occur. A comparison of the range maps shows that certain of the host species, i. e., *Castanea dentata*, *Fagus grandifolia*, *Quercus alba*, *Q. coccinea*, *Q. falcata*, *Q. Prinus*, *Q.*

rubra, and *Q. velutina*, extend well beyond the known range of *E. gyrosa*.

In considering the prevalence of a fungus, however, not only the occurrence of its hosts, but their relative abundance must be considered. In general, a fungus will be more abundant in a given locality the more numerous are the favorable hosts. The fact is generally recognized in horticultural practice that an isolated plantation is more likely to escape disease than one close to other similar plantations. It is to be expected then that *E. gyrosa* would be found most abundantly where its favorite hosts are most numerous, and this is actually the case.

FOREST REGIONS

A glance at the map of the forest regions of the United States issued by the Forest Service shows that the region in which *E. gyrosa* is most abundant comprises the southern forest and portions of the central forest. The following brief descriptions of the three forest regions under consideration are taken from the Forest Service map of the "Forest Region of the United States," issued in 1910:

Northern forest (northern portion): White, red and jack pines, spruces, firs (balsam), poplars and aspens, birches, tamarack.

(Southeastern portion): Maples, beech, birches, aspen, chestnut, white, red, and scrub pines, spruces, fir (balsam), hemlocks, tamarack, arbor-vitae.

Central forest. White, black and red oaks, hickories, chestnut, walnut, and butternut, yellow poplar, cherry, ashes, elms, maples, beech, locust, buckeyes, cottonwood.

Southern forest. Yellow pines, white, live, red, and black oaks, hickories, cypresses, white cedar, juniper, red and tupelo gums, magnolias, bays, elms, hollies, ashes.

In both the forest regions in which *E. gyrosa* is abundant, its favorite hosts, white, black and red oaks (*Quercus* spp.), together with beech (*Fagus*), in the central forest, and red gum (*Liquidambar*) in the southern, are included among the characteristic species.

In the northern forest beech is the only host of *E. gyrosa* mentioned among the characteristic trees, and even beech only in the southern portion. It is evident then that though several

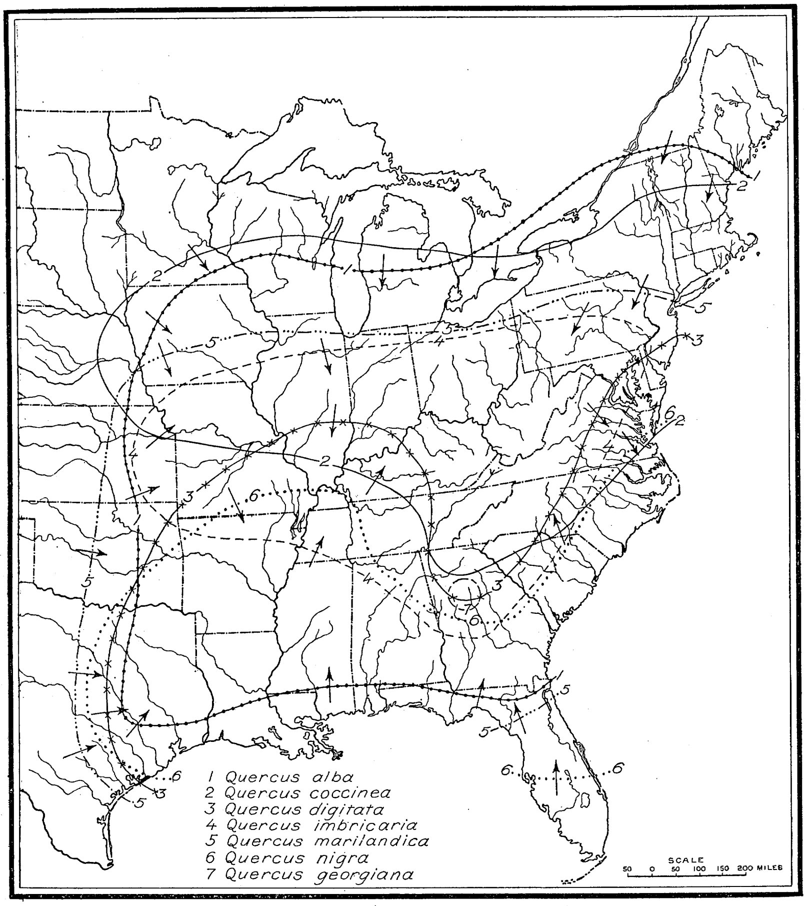

FIG. 3. Ranges of several species of *Quercus* in the United States. Map prepared by W. H. Lamb.

of the host species of *E. gyrosa* extend considerably north of the region where this fungus has been found they no longer predominate.

The relative importance of hosts of *E. gyrosa* among the northern hardwoods is well brought out in a recent report by Frothingham (3, p. 6), in which the species comprising the northern hardwood forest are grouped according to their prevalence as characteristic, locally characteristic, or occasional. Of the hosts of *E. gyrosa* only beech appears among the characteristic and only

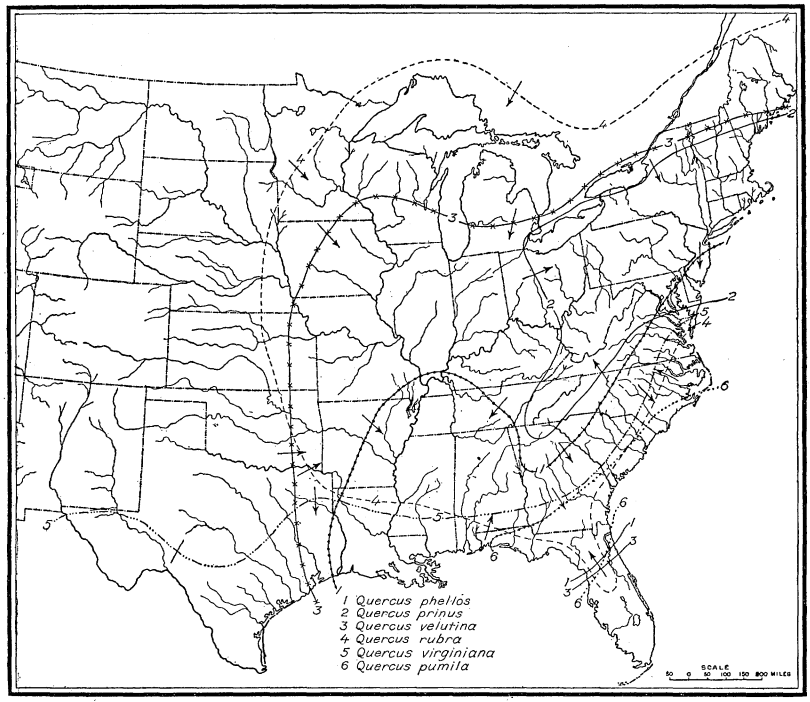

FIG. 4. Ranges of several other species of *Quercus* in the United States. Map prepared by W. H. Lamb.

red oak among the locally characteristic species. It is suggestive that in only one locality, Central Michigan, has *E. gyrosa* been found in the northern forest, especially as that region in New York, Pennsylvania, Maryland, and adjoining portions of West Virginia has been the scene of much recent collecting in connection with work on chestnut blight. There seems to be no climatic reason why *E. gyrosa* should not occur on beech in the northern states of New England, and the writer believes it may yet be found there. Host relations alone would, however, prevent its becoming prevalent.

SOIL RELATIONS

Within the Central and Southern Forest Regions where its hosts are abundant, the relative amount of opportunity for infection is greatly influenced by soil and cultural conditions. As has already been mentioned, exposed and injured roots of *Fagus* and

Quercus are by far the most favorable places for infection of *E. gyrosa*. In the southern states climatic and cultural conditions combine to make such exposed roots very much more common than in the northern states.

EROSION

The difference in soil erosion alone would largely account for the much greater abundance of exposed roots in the south. While no accurate data as to the relative erosion in various parts of the country are at hand, a review of the literature of the subject

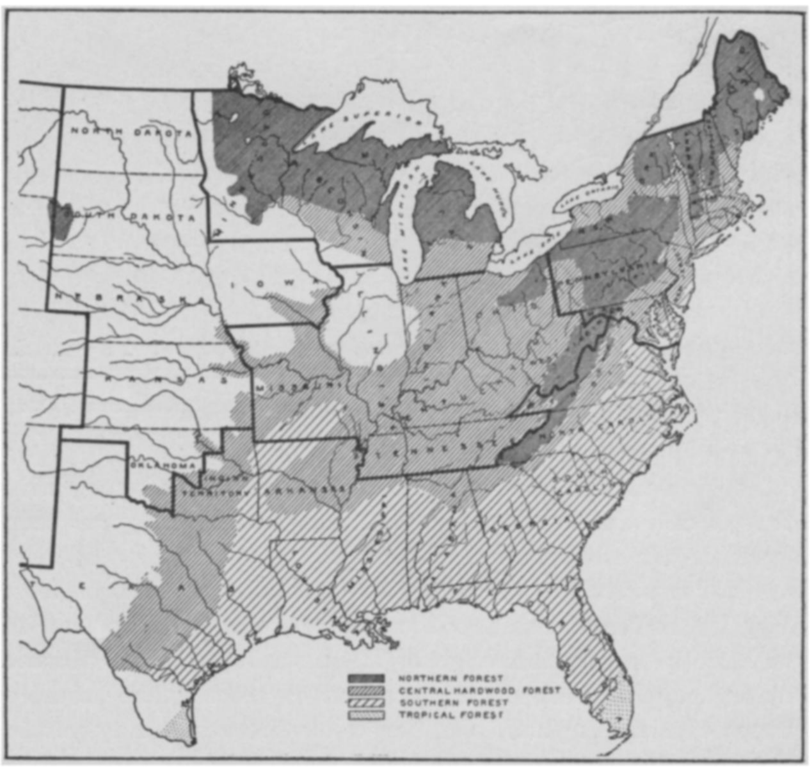

FIG. 5. Forest regions of the eastern United States. Map supplied by United States Forest Service.

shows clearly that in the states of Virginia, Kentucky, Tennessee, North and South Carolina, Alabama, Georgia, Louisiana, and Arkansas soil erosion is a serious problem. Davis in a recent review (2) of the subject calls attention to the fact that throughout

the south erosion is worse than in other sections of the country and suggests that "it is probable that the climate has much to do with the fact that erosion is so rapid in the south. The character of the soil makes a marked difference in the rates of erosion under the same climatic conditions."

SNOW-COVER

The abundant rainfall of the southern states, already referred to, no doubt greatly increases erosion. Perhaps equally important is the amount of snowfall, or rather the persistence of snow-cover, since the longer the period during which the ground is covered with snow, the shorter the period of soil erosion.

The snowfall data of the U. S. Weather Bureau are not so arranged as to show readily the period each year for which the ground is covered with snow in any given locality. Recently, however, Brooks published a discussion (1) of the snowfall of the eastern United States in which he reviewed the previous work on the subject and summarized the available data. Brooks also maps the average snowfall for each month, the average annual snowfall in inches, and the average annual number of snowfall days in the eastern United States. From these maps it is possible to get a fairly good idea of the duration of snow-cover in various parts of the region under consideration.

While the total amount of snowfall does not necessarily correspond with duration of snow-cover, in general those regions which have most snow have the longest periods of frozen and snow covered ground, and the shortest periods in which erosion is possible. Certainly soil in the region which has an average of over twenty inches annual snowfall and one inch as early as November is more protected than that south of this region. Longer snow-cover alone would greatly reduce the amount of erosion in the northern states as compared with that in the south. Greater erosion means necessarily more exposed roots and consequently more frequent opportunity for infection with *E. gyrosa*.

CULTURAL CONDITIONS

The contrast between the cultural conditions of the north and south has been frequently noted (4, 9). The relation of cul-

tural conditions to erosion is aptly described by Spillman (9, p. 260) as follows:

> The northern half of the country has always been more or less covered with various grasses. These have prevented soil erosion except in small isolated areas; but in the South where a single-crop system with clean culture has been the rule, and where in consequence, the soils have been left bare during the winter, soil erosion has been an important factor, especially where the land is more or less rolling or hilly.

The effect of the cattle industry in increasing the opportunity for infection and thus in all probability the abundance of the fungus in southern Indiana and Ohio has already been mentioned. And from the beginning of our collecting, the unfenced public squares of the southern towns where stock is permitted to graze have proven most favorable localities for the growth of *Endothia gyrosa*.

In brief, the writer believes that while the occurrence of *E. gyrosa* may be limited by climatic factors which are not yet determined, its prevalence in the southeastern states is caused by the great opportunities for infection in that region, due to the combined influence of host, soil, climatic and cultural conditions.

SUMMARY

Endothia gyrosa, which has a wider known range in America than any other species of the genus, is undoubtedly indigenous, having first been collected by Schweinitz nearly a century ago.

Although found in widely separated localities in the United States it is abundant only in the Southeastern States. Range maps of this and other American species of *Endothia* based on two years' collecting by Dr. C. L. Shear and the writer have already been published.

Inoculation experiments conducted in 1914 and 1915 showed that *E. gyrosa* would under certain conditions grow and winter over beyond the northeastern limits of its known range as well as within the region where it is abundant.

These inoculation experiments emphasized the importance of the water supply and of the condition of the host in the growth of the fungus.

E. gyrosa grows most readily on injured tissue which does not dry out immediately but remains living for some time, such as stubs of cut limbs or injured roots.

The temperature of the Southern States is undoubtedly more favorable for the growth of *E. gyrosa* than that of the states farther north.

The northern boundary of the region where this fungus is abundant does not, however, agree closely with that of any of the temperature regions.

It is not perceptibly more abundant in the areas of nine to twelve months vegetation than it is in areas of seven months vegetation.

Much of the area where *E. gyrosa* is abundant is in or south of the region of 25 inches rainfall, April to September, inclusive. It is, however, very abundant in Tennessee, Kentucky, and Indiana, where the rainfall is less than 25 inches for this period.

Although there are no sudden changes in climate in going from north to south in the eastern United States, there is a fairly definite division into an area where *E. gyrosa* is abundant and an area where it is rare.

This seems to indicate that factors other than climate affect the prevalence of this fungus.

The chief factor in the greater abundance of *E. gyrosa* seems to be increased opportunity for infection.

Opportunity for infection is much greater in the Southern States than in the Northern because of the larger number of host species and their greater importance relative to other species.

Opportunity for infection is still further increased by the soil and cultural conditions which cause greater erosion and leave large numbers of roots of *Fagus* and *Quercus* exposed and subject to injury.

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